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THE CHEMICAL SYSTEMATICS OF COLONIAL MARINE ANIMALS: AN ESTIMATED PHYLOGENY OF THE ORDER GORGONACEA BASED ON TERPENOID CHARACTERS

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Abstract

The classification of colonial marine invertebrates is often very difficult. The purpose of this paper is to illustrate the potential of numerical chemotaxonomy and cladistic analysis to facilitate the study of the evolution of these organisms. Chemotaxonomy has contributed little to the study of these animals, in spite of the large amounts of data generated by marine natural products chemistry. Existing chemosystematic investigations of colonial animals have not employed the methods of numerical taxonomy or of cladistic analysis. As an example of the usefulness of such an approach, cladistic analysis on quantified chemical data was performed for nineteen species of gorgonians. This produced cladograms which, for the most part, agreed with classical gorgonian systematics, but which also yielded several new insights into the evolution and classification of gorgonians. Numerical chemotaxonomy and cladistic analysis should not continue to be ignored as a tool for the study of phylogenetic relationships among groups of colonial marine invertebrates.

Introduction

The classification of colonial marine invertebrates such as the Porifera (sponges) and the Alcyonaria (octocorals) is often problematical (deLaubenfels, 1936: Bayer, 1961; Wiedenmayer, 1977). These organisms usually lack a well-defined, consistent form. Classifications are based on morphological characters such as color, general growth pattern, polyp morphology (in the Alcyonaria), and particularly the arrangement, color, size, and shape of spicules (Bayer, 1961; Wiedenmayer, 1977). The genetic basis of these characters is unknown, and the environment can exert significant influences on their expression (Bayer, 1961; Grigg, 1970; Kinzie, 1973; Simpson, 1978). Furthermore, the fossil record of most colonial marine invertebrates is incomplete. These problems make it difficult to establish genealogical affinities among the living representatives of these groups.

Chemotaxonomy—the construction of classifications using chemical compounds as characters—could provide new insights into the systematics of colonial marine animals. Both the Porifera and the Alcyonaria possess a diverse array of chemical compounds and are particularly rich in isoprenoids, including terpenes, carotenoids, and steroids (Fenical, 1978 and 1982; Goad, 1978; Tursch *et al.*, 1978; Bergquist, *et al.*, 1980; Liaaen-Jensen *et al.*, 1982). (For a discussion of the possible ecological roles of these compounds in coelenterates, see Tursch *et al.*, 1978). Each species of sponge and octocoral seems to have its own specific set of compounds (Ciereszko and Karns, 1973: Kashman *et al.*, 1980). Marine natural products chemistry has progressed to the point where it is often easier to identify compounds from

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colonial marine organisms than it is to identify the animal from which the compounds were isolated (Faulkner, 1977). In spite of this, chemotaxonomy has contributed little to the study of colonial marine animals. A few chemotaxonomic studies of sponges have been performed (see, for example, Bergquist *et al.*, 1980), but no such studies have been undertaken with octocorals. Existing chemotaxonomic studies of colonial marine invertebrates have not employed the methods of numerical taxonomy, even though chemical characters can be exactly described (Holger, 1968) and thus lend themselves to numerical analysis.

As noted earlier, establishing evolutionary affinities among groups of colonial marine invertebrates is difficult. Cladistic analysis is a technique which allows one to infer phylogenetic relationships from the characters of extant species (Farris *et al.*, 1970; Farris, 1973). A combination of numerical cladistic analysis and chemotaxonomy should greatly facilitate the study of phylogenetic relationships among groups of colonial marine invertebrates. As an example of the application and potential value of such an approach, I performed cladistic analysis on quantified chemical data for nineteen species of gorgonians. Hopefully, this paper will illustrate the immense potential of numerical chemotaxonomy and cladistic analysis for improving our understanding of the evolution of colonial marine invertebrates.

Materials and Methods

Tursch *et al.* (1978) described the absolute configuration and species distribution of twenty-eight terpenoid compounds isolated from nineteen species of gorgonians. This data set was used in the present study because the chemical structures presented in it had previously appeared in the literature and were regarded by Tursch *et al.* to be accurate. This information was arranged into a 19 × 28 matrix of ones and zeros, with columns of the matrix corresponding to chemical compounds and rows corresponding to gorgonian species. An entry of "1" in a row and column indicated that the species possessed that particular compound, while a "0" denoted the absence of the compound (see Table I). Cladograms were generated from this matrix by computer using the method of Farris *et al.* (1970).

The carbon skeletons of the compounds were then examined and placed into seventeen biosynthetic categories, based on the pathways of terpenoid biosynthesis outlined by Herout (1971) and Fenical (1978). The bicyclic compounds eunicellin and briarein A were not classified as cembranoid diterpenes. These compounds may arise via unusual cyclizations of geranylgeraniol pyrophosphate instead of a further cyclization of the 14-membered ring of a cembranoid precursor [Fenical, 1978]. Two alcyonacean genera, *Clavularia* and *Cespitularia*, produce tricyclic or bicyclic compounds apparently via an unusual cyclization of geranylgeraniol pyrophosphate [Coll, 1980]. To my knowledge, experimental data on the biosynthesis of eunicellin and briarein A do not exist. The classification of these compounds as non-cembranoids does not drastically alter the position of *Eunicella stricta* or *Briareum asbestinum* in the cladograms.) The presence or absence of a particular class of compounds was noted for each of the 19 gorgonian species. This information was arranged into a 19 × 17 matrix of ones and zeros analogous to the presence-absence data matrix (see Table II), and then generated cladograms from the matrix.

Finally, the presence-absence data matrix was combined with the biosynthetic data matrix to produce a 19 × 45 matrix of ones and zeros. This matrix was also used to generate a series of cladograms.

All cladograms were rooted by adding an all-absent ancestor, a hypothetical ancestor which lacked all terpenoid compounds.

TABLE I

Presence-absence data matrix

	(+)-α-Bisabolene	(+)-β-Bisabolene	(−)-α-Curcumene	(+)-β-Curcumene	(−)-β-Curcumene	(−)-Germacrene	(−)-δ-Cadinene	(+)-α-Muurolene	(+)-β-Gorgonene	(+)-γ-Maaliene	(−)-1(10)-Aristolene	(+)-9-Aristolene	(+)-α-Copaene	(+)-β-Copaene	(+)-α-Cubebene	(+)-β-Elbourbonene	Allaromadendrene	Furoventlene	Asperdiol	Crassin acetate	Eupalmerin acetate	Eunicin	Jeunicin	Peunicin	Cueunicin	Cueunicin acetate	Eunicellin	Briarein A
Briareum asbestinum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eunicea asperula	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Eunicea mammosa	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0
Eunicea palmeri	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0
Eunicea succinea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
E. succinea var. *plantaginea*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eunicea tourneforti	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0
Eunicella stricta	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Gorgonia ventalina	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Muricea elongata	1	0	1	0	1	0	0	1	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Plexaurella dichotoma	1	1	1	1	0	0	0	1	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Plexaurella fusifera	1	1	1	1	0	0	0	1	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Plexaurella grisea	1	1	1	1	0	0	0	1	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Plexaurella nutans	0	1	1	1	0	0	0	1	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Pseudoplexaura crucis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0
Pseudoplexaura flagellosa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0
Pseudoplexaura porosa	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0
Pseudoplexaura wagenaari	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0
Pseudopterogorgia americana	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1

TABLE II

Biosynthetic data matrix

	Farnesanes	Bisabolanes	Germacranes	Bicyclogermacranes	Maaliianes	Gorgonanes	Aristolanes	Cadinanes	Copaanes	Cubebanes	Bourbonanes	Aromadendranes	Furoventalanes	Geranylgeranyls	β-cembranoids	Briareins	Eunicellins
Briareum asbestinum	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0
Eunicea asperula	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0
Eunicea mammosa	1	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0
Eunicea palmeri	1	0	1	0	0	0	0	1	1	0	0	0	0	1	1	0	0
Eunicea succinea	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0
E. succinea var *plantaginea*	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0
Eunicea tourneforti	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0
Eunicella stricta	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
Gorgonia ventalina	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Muricea elongata	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Plexaurella dichotoma	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Plexaurella fusifera	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Plexaurella grisea	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Plexaurella nutans	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pseudoplexaura crucis	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0
Pseudoplexaura flagellosa	1	0	1	1	0	0	0	1	1	1	1	1	0	1	1	0	0
Pseudoplexaura porosa	1	0	1	1	0	0	0	1	1	1	1	1	0	1	1	0	0
Pseudoplexaura wagenaari	1	0	1	1	0	0	0	1	1	1	1	1	0	1	1	0	0
Pseudopterogorgia americana	1	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0

RESULTS

The most parsimonious cladograms generated from the presence-absence data matrix, from the biosynthetic data matrix, and from the combined data matrix were selected. This was accomplished by choosing from each series of cladograms, the cladogram with the shortest total length, the lowest F-ratio, and the highest index of consistency. This corresponds to selecting the cladogram which postulated the smallest amount of parallel evolution. (The total length, the F-ratio, and the index of consistency all provide some information on the number of evolutionary reversals contained in a cladogram. For definitions of these measures and for further discussion of their interpretation, see Kluge and Farris [1969], Farris [1972], and Prager and Wilson [1978].) All of these measures suggest that the chemotaxonomic data used here are highly consistent; that is, the amount of parallel evolution which must be postulated to explain the data, was fairly low. The selected cladograms corresponding to the presence-absence data matrix, the biosynthetic data matrix, and the combined data matrix are shown in Figures 1, 2, and 3, respectively. Each line connecting two nodes on the cladogram, or connecting a node with a gorgonian species, is known as a "branch." The nodes of the cladogram denote hypothetical ancestors. The numbers on the branches are known as "branch lengths," which in this case are simply the number of characters not common to both points connected by the branch.

All three cladograms agree remarkably well with Bayer's (1961) classification

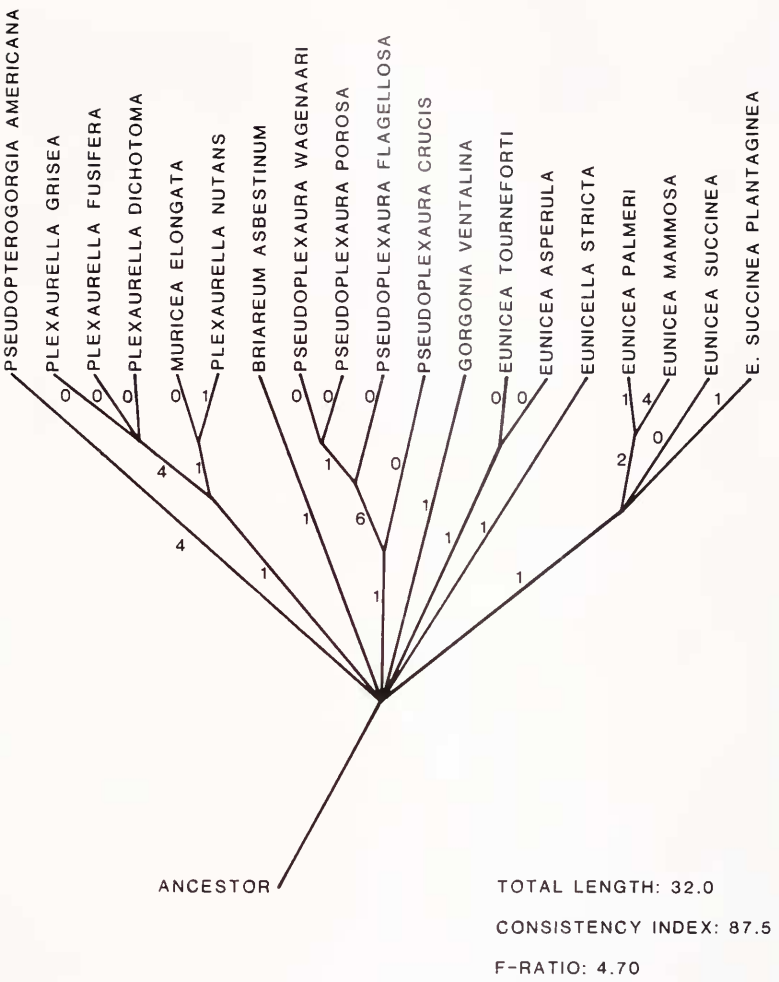

FIGURE 1. Cladogram 1, generated from the presence-absence data matrix.

of gorgonians (Table III). In all cladograms, congeneric species tend to group together. One cannot usually infer intergeneric relationships from the presence-absence data ("Cladogram 1"). Such inferences can be made in the cladograms generated from the biosynthetic data matrix and the combined data matrix ("Cladogram 2" and "Cladogram 3," respectively), indicating that the addition of biosynthetic data provides a great deal of information on the relatedness of genera.

In Cladograms 2 and 3, *Briareum asbestinum*, which is placed by Bayer (1961) and Kukenthal (1924) in the suborder Scleraxonia (Table III), does not group closely with species of the other gorgonian suborder, the Holaxonia. Furthermore, the genera *Pseudopterogorgia* and *Gorgonia* tend to be separated from the other gorgonian species. Bayer (1961) places these genera in a separate family, the Gorgoniidae.

Eunicella stricta possesses the unusual terpenoid eunicellin and hence shows no close affinities with other gorgonian species in Cladograms 1, 2, or 3. This genus is also peculiar in morphology (even though it is classically placed in the family Plexauridae), having an unusual growth form and possessing "balloon-club" spicules

TABLE III

Classification of the genera examined in this paper, using the taxonomy of Bayer (1961)

Order Gorgonacea
Suborder Scleraxonia
Family Briareidae
Genus *Briareum*
Suborder Holaxonia
Family Plexauridae
Genus *Plexaurella*
Genus *Pseudoplexaura*
Genus *Eunicea*
Genus *Eunicella*
Genus *Muricea*
Family Gorgoniidae
Genus *Gorgonia*
Genus *Pseudopterogorgia*

which are unique to this genus (Bayer, 1961). Thus, both chemical and morphological evidence suggest that *Eunicella stricta* is markedly different from the other species used in this study.

The terpenoid data suggest that the genus *Eunicea* should be split into two groups, one containing *Eunicea asperula* and *E. tourneforti*, and the other containing *E. mammosa*, *E. palmeri*, *E. succinea*, and *E. succinea forma plantaginea*. This split corresponds exactly to two subgenera, the subgenus *Eunicea sensu strictu* and the subgenus *Euniceopsis*, proposed by Bayer (1961) on the basis of anthocodial spiculation. Bayer (1961) stated that "future work may demonstrate that these subgenera are actually of full generic importance." Examination of Cladogram 3 shows that the patristic distances (the sum of lengths of branches connecting two taxa—see Farris, 1967) between *Eunicea tourneforti* (or *E. asperula*) and members of the "*Euniceopsis*" subgroup range from 2 to 10, with a mean distance of 6. This suggests that *E. tourneforti* and *E. asperula* are no more closely related chemically to the "*Euniceopsis*" species than they are to species of other genera. Thus, the chemical data considered here support the idea that *Euniceopsis* and *Eunicea sensu stricto* should be elevated to the level of genera.

Cladogram 2 and Cladogram 3 suggest that the order Gorgonacea is comprised of two major evolutionary clades (Fig. 2 and 3). One clade contains the genera *Gorgonia*, *Pseudopterogorgia*, *Plexaurella*, and *Muricea*, all of which possess sesquiterpenes but lack diterpenes. The second clade consists of the genera *Briareum*, *Eunicella*, *Eunicea*, and *Pseudoplexaura*, which all contain diterpenes. Within this latter clade, *Eunicea mammosa*, *E. palmeri*, *Pseudoplexaura flagellosa*, *P. porosa*, and *P. wagenaari* form a sub-clade of species with sesquiterpenes as well as diterpenes. The species of the sub-clade seem to have evolved independently the ability to synthesize large quantities of sesquiterpenes. This implies that the family Plexauridae is diphyletic (see Fig. 3).

There are three groups of chemically indistinguishable species. The first group consists of *Plexaurella fusifera*, *P. dichotoma*, and *P. grisea*; the second contains *Eunicea tourneforti* and *E. asperula*; and the third includes *Pseudoplexaura porosa* and *P. wagenaari* (Fig. 3). Bayer (1961) noted that until further study delineated the range of variability of octocoral species, "the taxonomy of the octocorals will remain in confusion, cluttered with superfluous 'species' that are mere variants of one." The chemical data considered here suggest that each of the three groups should

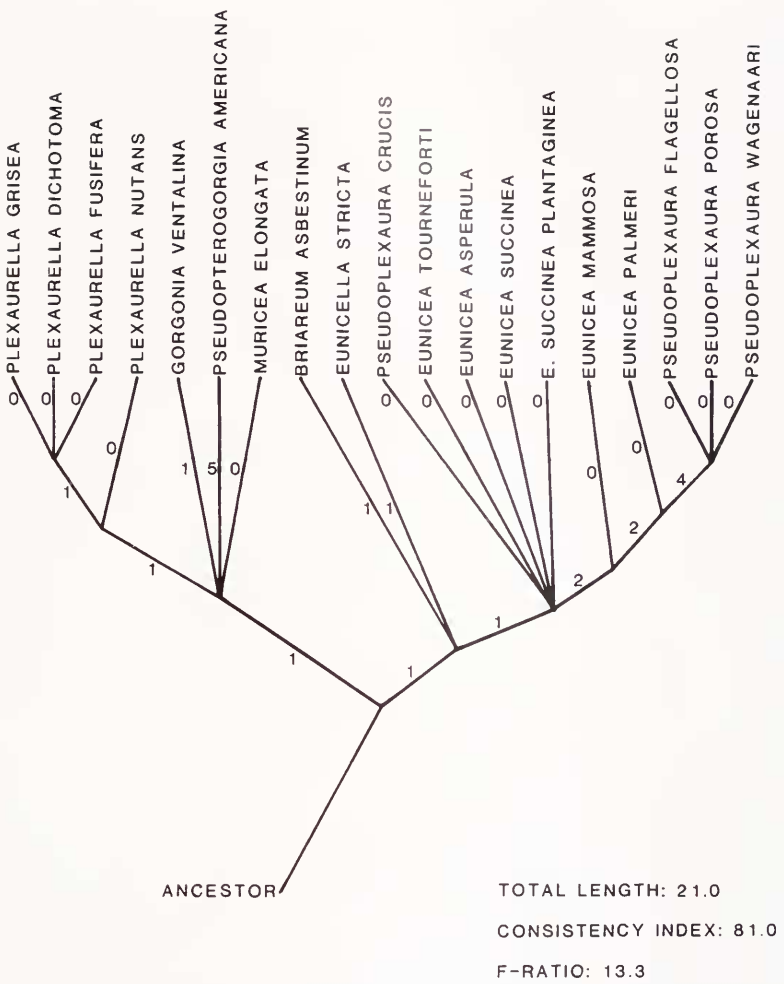

FIGURE 2. Cladogram 2, generated from the biosynthetic data matrix.

be consolidated into three species, each containing several variants which correspond to the classical "species." The possibility exists that these species have become reproductively isolated without any divergence occuring in their chemical content. These species should be examined more carefully to ascertain whether they are true species or whether they are simply variants.

DISCUSSION

In general, the chemically based cladograms agree very closely with classical gorgonian taxonomy. Frequently found, for a wide variety of organisms, is a close fit between classifications based on biochemical data and those based on morphological information (Ferguson, 1980). Further work on the biochemical taxonomy of gorgonians will probably provide a great deal of support for Bayer's (1961) classification, while providing several new insights into gorgonian systematics and evolution.

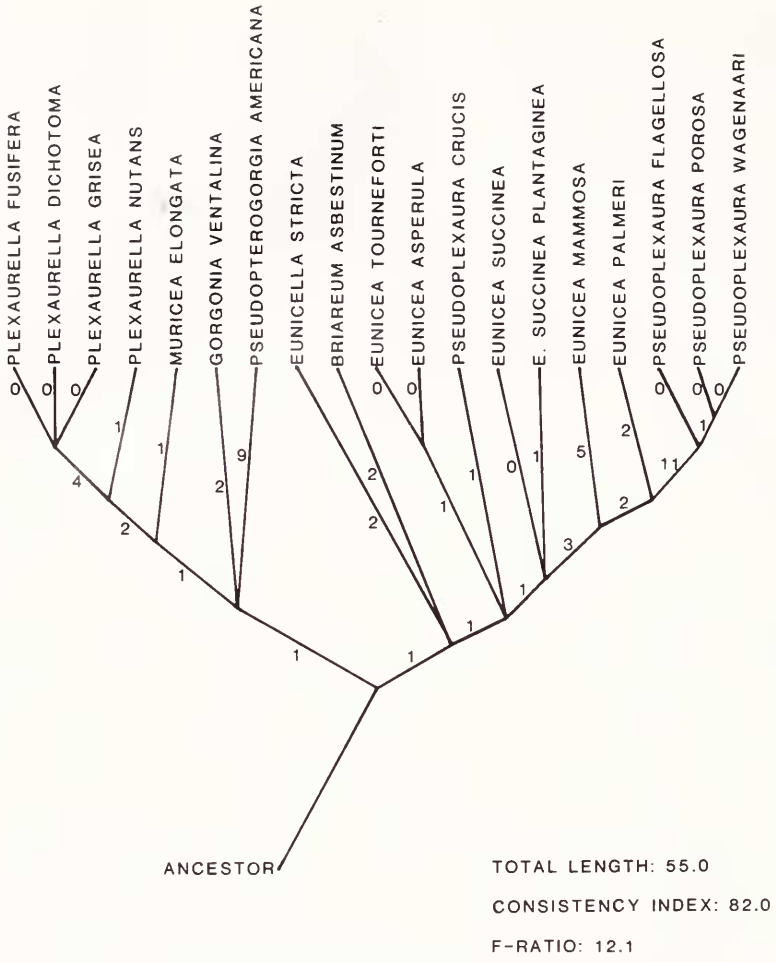

FIGURE 3. Cladogram 3, generated from the combined data matrix.

The classical systematics of gorgonians and other colonial marine invertebrates is based heavily on morphological characters (Kukenthal, 1924; De Laubenfels, 1936; Bayer, 1961; Wiedenmayer, 1977). For gorgonians, spicule morphology and the general growth form of the colony are the characters most frequently used for classification (Bayer, 1961; Grigg, 1970). The degree to which variation in these characters reflects genetic differences between colonies is unknown (Bayer, 1961). However, spicule shape and size can vary considerably within a single gorgonian colony (Bayer, 1961). Several studies have shown that the growth form of a gorgonian can be greatly affected by currents (Wainwright and Dillon, 1969; Grigg, 1970; Kinzie, 1973). Grigg (1970) showed that there was considerable geographic variation in spicule and colony morphology within the gorgonian species *Muricea californica* and *M. fruticosa*. (The variation was so great that Grigg [1970] suggested that they might be different variants of a single species.) When Kinzie (1973) transplanted colonies of *Eunicea clavigera* and *Gorgonia mariae* from deep water to shallow water, he found that spicules near the growing tips of the colonies began to exhibit abnormal characters; furthermore, the spicules of transplanted *G. mariae* changed

color from white to red. Simpson (1978) demonstrated that the sponge *Microciona prolifera* produces thicker spicules at lower temperatures. Thus, the environment may have considerable effects on the morphology of gorgonians and perhaps other colonial marine invertebrates. As Bayer (1961) noted, gorgonian taxonomy will remain confused until the normal range of variation of systematically important characters and the effects of the environment upon them have been thoroughly documented.

At present we also know little about the geographic variation of terpenoids in gorgonians. Systematic studies of spatial or temporal variation of terpenoid content of gorgonians have not been undertaken, nor have the environmental effects on chemical content been clarified. In their review of terpenoids in coelenterates, Tursch *et al.* (1978) noted that the gorgonians *Pseudoplexaura porosa*, *P. wagenaari*, and *P. flagellosa* collected from a broad geographic area were very similar in their terpenoid content, while *Eunicea mammosa* yielded the diterpenes cueunicin, cueunicin acetate, eunicin, jeunicin, or eupalmerin acetate depending on where the colonies were collected. *E. mammosa* also showed geographic variation in its content of sesquiterpenes (Ciereszko and Karns, 1973). Tursch *et al.* (1978) reported that similar geographic variation occurs in *Eunicea palmeri* and *E. succinea*. Long-term variation of diterpene content through time also seems to exist in some gorgonians. Within one area in Jamaica, *E. mammosa* contained only jeunicin, while colonies collected from Jamaica in later years contained mixtures of both jeunicin and eunicin (Tursch *et al.*, 1978). *Briareum asbestinum* from one collection yielded briareins A and B, but a collection of this species in the same location one year later yielded briareins C and D. It is possible that chemical content of colonial marine animals varies with the age or reproductive status of the colony. The amount of lipid in the sponge *Haliclona permollis* varies seasonally, and the fluctuations may be related to the reproductive cycle of the colony (Elvin, 1979). Initial studies of terpenoids in the alcyonacean *Capnella imbricata* suggested that seasonal variation in the chemical content of this species may occur (Tursch *et al.*, 1978). More detailed studies of temporal variation in the terpenoid content of colonial marine animals have not been reported. Interestingly spatial and temporal variation in the chemical content of a colonial coelenterate is due to changes in the chemical functionalization of the terpenoid skeleton, not to changes in the skeleton itself (Tursch *et al.*, 1978). Approaches such as the one employed in this paper, which emphasize the importance of the basic carbon skeleton of a terpenoid rather than the presence of certain functional groups in the compound, should reduce the problems posed by geographic and temporal variation in chemical content.

Thus, biochemical characters are subject to some of the same criticisms as morphologic characters. However, biochemical characters are probably better reflections of the genetic differences between species than are morphological characters such as spicule shape. Terpenoids are fairly direct reflections of the action of certain biosynthetic enzymes, which in turn are reflections of the presence of particular genes in the organism. Spicules, on the other hand, are complex structures of calcium carbonate (or silica in the Demospongiae) and are the endproducts of an intricate network of physical processes, each of which may be influenced directly or indirectly by many genes, and which may perhaps be strongly affected by the physical environment.

The paucity of knowledge of the biosynthesis of marine natural products presents another problem for chemotaxonomy. This study has used a biosynthetic scheme for the sesquiterpenes (Herout, 1971) which may or may not represent the pathways operating in gorgonians. (Since use of these biosynthetic pathways leads to clado-

grams which closely fit classical gorgonian systematics, the scheme of Herout [1971] may actually be valid for the order Gorgonacea.) It may be argued that different species of colonial marine invertebrates could use different biosynthetic pathways to produce the same terpenoid compound. This, however, runs counter to present knowledge of terpenoid biosynthesis in other animals and plants. Clayton (1970) stated that the biosynthetic cyclizations of terpenoids "in general conform to patterns that can be rationalized in terms of non-enzymatic organic chemistry." Thus, in general, two organisms which produce the same type of terpenoid compound will do so via the same biosynthetic pathway. However, the enzymes which catalyze the reactions of the pathway may not be homologous; *i.e.*, the ability of two species to synthesize the same terpenoid may be due to parallel evolution. Cladistic analysis allows parallelism by assuming that characters are reversible (Kluge and Farris, 1969), but if parallelism is rampant, it can cause great difficulties in estimating evolutionary affinities. The cladograms generated in this study for the most part closely fit the classical hierarchy of gorgonian taxonomy, suggesting that parallel evolution of terpenoids is not rampant, and that terpenoid compounds are indeed good characters to use in establishing a taxonomy. These conclusions are also supported by the high degree of consistency of the chemical data. Detailed knowledge of the biosynthesis of compounds in colonial marine animals could provide a great deal of information on the evolution of these organisms. Additional work must be done before this becomes feasible.

The cladograms generated in this paper are based on a limited amount of published chemical data. They are not meant to be serious challenges to accepted gorgonian taxonomy. However, they do suggest several places where classical systematics may be in error and where further work may be warranted. Numerical chemotaxonomy and cladistics could help to clear up many areas of confusion in the classification of colonial marine invertebrates, especially if chemical data were coupled with morphological information. This study is meant to illustrate the great potential of numerical chemotaxonomy for the study of the systematics and evolution of colonial animals. This tool should not continue to be ignored.

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